SPECIES HYBRIDS IN PLATANUS AND CAMPSIS

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With two text figures

ACCORDING TO SEWARD (1931), *Platanus* is one of the oldest of broad-leaved trees, and fossil types have been found which are very similar to the fertile branches of modern species. This genus was one of the most widely spread of the earlier cretaceous dicotyledons. The cretaceous *Platanus* was more variable and had a much wider distribution than the existing species.

The genus *Platanus* is now found in North America to Mexico and from southeastern Europe to India (Rehder, 1927). The American species, *P. occidentalis,* is hardier than the Old World species, *P. orientalis;* but the two species must be rather closely related because they have produced the fertile hybrid *P. acerifolia.* According to Henry and Flood (1919), *P. acerifolia* originated as a natural hybrid between the Occidental and Oriental Plane. It probably originated in the Oxford Botanic Garden about 1670. The hybrid is intermediate in leaf and fruit characters and seems to possess unusual vigor. The hybrid is extensively used for planting in the streets of European towns where neither of the parental species will survive. Seedlings from the hybrid are variable, some of them resembling the parental species.

The fact that the species hybrid is fertile, and segregates in the second generation, would indicate that the parental species have the same number of chromosomes and that their chromosomes are similar. The haploid chromosome number of *Platanus* has been reported to be 21 (Winge, 1917), 8 (Brouwer, 1924), and 20-22 (Bretzler, 1924). Permanent smear preparations of pollen mother cells from *P. occidentalis* and *P. acerifolia* show clearly that the number of chromosomes is 21, as reported by Winge. The chromosomes are paired regularly at the first meiotic division, and there is no evidence of lagging chromosomes at any stage in the meiotic divisions. The chromosomes at the first meiotic metaphase, and at telophase, in the hybrid, are represented in Figure 1. One of the chromosomes is somewhat smaller than the others, especially when fixed in aceto-carmine solution. The chromosomes are too small and numerous to permit an accurate determination of chiasma frequency, but both rod and ring chromosomes were observed. The average chiasma frequency is about 1.5 per bivalent. About 90 percent of the pollen is good in the hybrid.

The apparent compatibility of the chromosomes from the two parental species in the first generation hybrid indicates that the Old and New World species have undergone no very fundamental changes since their segregation and differentiation. Although this genus has undergone no very fundamental changes for a long period of time, and even though it is one of the oldest dicotyledons so far discovered, it does not possess characters which mark it as a primitive type or as an early member of an evolutionary series (Seward, 1931). It is of interest that *Platanus* is the only genus of the family Platanceæ.

Another valuable hybrid between species from the Old and New World is *Campsis Tagliabuana* (*C. hybrida*) (Rehder, 1932). The parental species are *C. radicans,* from central and southern United States, and *C. chinensis,* from China. The American species seems to

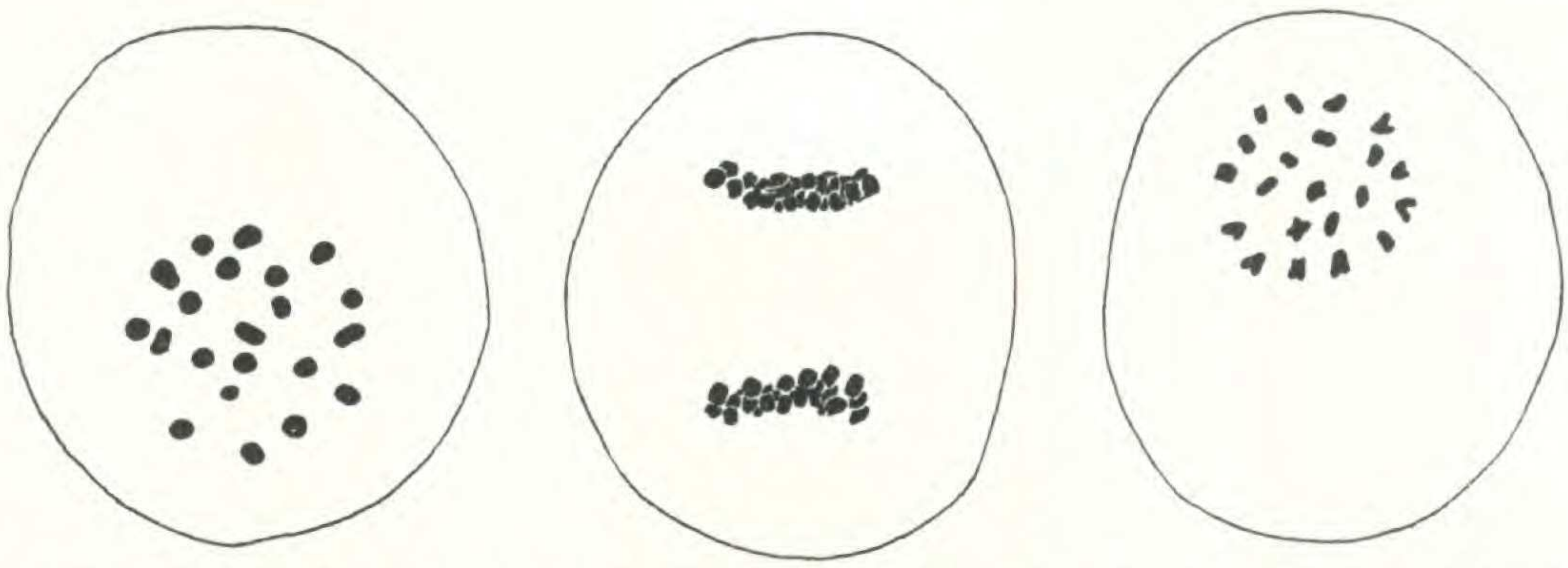

FIGURE 1. Meiotic chromosomes of *Platanus acerifolia* at metaphase and telophase. The 21 bivalents divide regularly. × 2000.

be hardier and more vigorous than the Chinese species, but the flowers of *C. chinensis* are more attractive. The hybrid has the good qualities of both parents. It is almost as attractive as the Chinese species and has the hardiness of the American species. The hybrid forms are grown in many gardens of southern Massachusetts (Anderson, 1933).

The hybrid was first recorded by Visiani as having been raised by the brothers Tagliabue apparently some time before 1859, but doubtless it has originated independently elsewhere afterwards or even before 1859. Natural hybrids have also been obtained at the Botanical Garden in Washington, D. C. A more complete account of the origin and characteristics of *Campsis Tagliabuana* has been presented in the Arnold Arboretum bulletin of popular information, by Edgar Anderson.

The hybrids are partially fertile, and numerous segregates have been produced. The chromosome number is undoubtedly the same for both the parental species and the hybrid. There are 20 pairs of small chromosomes at the first meiotic division in *C. radicans.* No representatives of *C. chinensis* were available for study, but a hybrid segregate much like the Chinese species, also has 20 pairs of chromosomes. The hybrid has 20 pairs of chromosomes which are perfectly regular in pairing and disjunction at meiosis. The chromosome number found in the hybrid is in accord with the count reported by de Vilmorin and Simonet (1927). The chromosomes are very small and usually form rod bivalents at the first meiotic division. The chiasma frequency is apparently little more than one per bivalent.

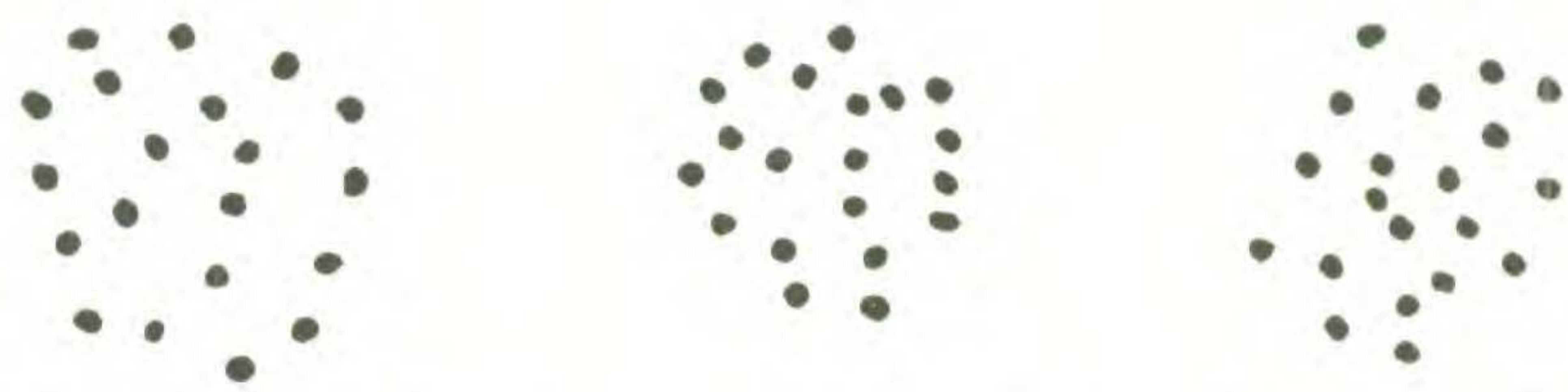

FIGURE 2. Meiotic chromosomes of *Campsis radicans*, *C. Tagliabuana* and *C.* spec. (probably a hybrid segregate resembling *C. chinensis*). The divisions are regular in the one parental species examined and in the hybrids. × 2000.

Although there is regular pairing and disjunction of the chromosomes in *Campsis Tagliabuana,* about 50 per cent of the pollen is sterile. There is less than 5 per cent pollen sterility in *C. radicans.* Pollen sterility in species hybrids which have regular meiotic divisions is also found in other genera (*Primula kewensis,* diploid, Newton and Pellew, 1929; *Deutzia* and *Philadelphus,* Sax, 1931; *Tradescantia,* Sax and Anderson, 1933). Pollen sterility in such species hybrids might be caused by unequal interchange of chromosome segments in one of the parental species. The interchange of segments between non-homologous chromosomes has been found in a considerable number of different genera in slightly related families, and may be much more extensive than is indicated by the formation of rings or chains of chromosomes. In a species with a low chiasma frequency, segmental interchange would not result in chromosome rings, and if segmental interchange were unequal, chromosome pairing would be regular in both heterozygous and homozygous forms. The heterozygous types will be eliminated unless they possess a much greater survival value to compensate for their partial sterility or unless balanced lethals are involved. As a result, plants should originate which are homozygous for segmental interchange chromosomes, as is known to be the case in *Datura, Pisum,* and *Oenothera.*

If an individual homozygous for two segmental interchange chromosomes (the minimum number possible) is crossed with a normal plant, the chromosomes should pair as bivalents and divide normally if the segmental interchange is unequal and if the chiasma frequency is low. But the random segregation of the chromosomes would result in 50 per cent non-disjunction of a chromosome segment. If both segments are essential for gametophyte development, the pollen sterility would be 50 per cent; if only the longer segment is essential, the pollen sterility would be 25 per cent. Pollen sterility would be almost complete in a plant heterozygous for four or five segmental interchange chromosomes.

Segmental interchange might well be one of the factors involved in the differentiation of species. A form with relatively few segmental interchange chromosomes would tend to be isolated from the normal type because of the sterility of the F_1 hybrid between the two forms. Unless lethal factors are associated with the segmental interchange chromosomes, the homozygous forms should have a higher survival value. Variations originating in the different lines homozygous for chromosome structure would not be swamped by intercrossing and would tend to be developed more or less independently in different structural genoms.

SUMMARY

Platanus acerifolia, a natural hybrid between *P. orientalis* of southeastern Europe and *P. occidentalis* of North America, has 21 pairs of chromosomes which pair regularly at meiosis. The hybrid is fertile, and genetic segregation occurs in the second generation. These facts indicate that the parental genoms are similar and are compatible with each other, even though the parental species have been isolated for a long period of time.

Campsis Tagliabuana, a natural hybrid between *C. chinensis* from China and *C. radicans* from North America, has 20 pairs of chromosomes which pair regularly at meiosis. Although the reduction divisions are regular, there is about 50 per cent pollen sterility in the F_1 hybrid. The association of regular chromosome pairing and partial or nearly complete pollen sterility in species hybrids may be the result of segmental interchange between non-homologous chromosomes in one or both parental species.

The species hybrids in the above genera contain the desirable characters of the parental species and are especially valuable because of their hardiness. Such hybrids are good illustrations of what may be expected from many hybrids between Old and New World species.

LITERATURE CITED

ANDERSON, EDGAR (1933). Trumpet-creepers. (Arnold Arb. Bull. ser. 4, **1**:1–5.)

BRETZLER, E. (1924). Beiträge zur Kenntnis der Gattung Platanus. (Bot. Arch. **7**:388–417.)

BROUWER, J. (1924). Studies in Platanaceae. (Rec. Trav. Bot. Néerl. **21**:369–382.)

HENRY, A., & M. G. FLOOD (1919). The History of the London Plane. (Proc. Roy. Irish Acad. **35**:9–28.)

NEWTON, W. C. F., & C. PELLEW (1929). Primula kewensis and its derivatives. (Jour. Genetics, **20**:405–467.)

REHDER, A. (1927). Manual of cultivated trees and shrubs. Pp. 930. (Macmillan Co., New York.)

———— (1932). Campsis Tagliabuana (Vis.), comb. nov. (Jour. Arnold Arb. **13**:340.)

SAX, KARL (1931). Chromosome numbers in the ligneous Saxifragaceae. (Jour. Arnold Arb. **12**:198–206.)

SAX, KARL & EDGAR ANDERSON (1933). Segmental interchange in chromosomes of Tradescantia. (Genetics, **18**:53–67.)

SEWARD, A. C. (1931). Plant life through the ages. Pp. 601. (University Press, Cambridge, England.)

VILMORIN, R. DE & M. SIMONET (1927). Nombre des chromosomes dans le genres Lobelia, Linum et chez quelques autres espèces végétales. (Compt. Rend. Soc. Biol. Paris, **96**:166–8.)

WINGE, O. (1917). The chromosomes, their numbers and general importance. (Compt. Rend. Trav. Labor. Carlsberg, **13**:131–275.)

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